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"The elms after 100 years of Dutch Elm disease"

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Ulmus laevis in the Iberian Peninsula: a review of its ecology and conservation

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European white elm (*Ulmus laevis* Pallas) populations are scarce, small and fragmented in the Iberian Peninsula. Due to these characteristics the indigenous status of the species in the region has been questioned, whilst the species' role in Iberian riparian forest ecology has been neglected. Herein we review past studies regarding this species' distribution and ecology in the Iberian Peninsula, with special emphasis on the establishment of conservation priorities. We first present a collection of palaeogeographic, historic and genetic data suggesting that the Iberian Peninsula was a glacial refuge for *U. laevis*. Secondly, we analyse *U. laevis* distribution in relation to soil physico-chemical properties and water availability in Spain. Following this, we focus on the reproductive biology of the species, and investigate the effect of masting and empty seed production on predation and regeneration establishment. Finally, based on this knowledge, we propose conservation policies for *U. laevis* in the Iberian Peninsula.

Keywords: Elm Conservation, Drought-stress Vulnerability, Root Iron Uptake, Population Genetics, Seed Dispersal, Seed Predation, *Ulmus laevis*' Distribution

Introduction

The European white elm (*Ulmus laevis* Pallas) is a hardwood deciduous tree which grows in river margins and damp bottomland forests, tolerating flooding for some periods

of the year (Collin et al. 2000). *Ulmus laevis* belongs to section *Blepharocarpus* (Wiegrefe et al. 1994), in contrast to the other two native European elms, *U. minor* Mill. and *U. glabra* Huds., which belong to the *Ulmus*

section. *Ulmus laevis* has been considered to be naturally distributed across Europe, from Ural Mountains to eastern France, and from southern Finland to the Caucasus, Balkans and southern France (Collin 2003). The loss of suitable habitats due to human-induced changes in riparian forests, combined with the effect of Dutch elm disease (DED), has compromised the survival of many *U. laevis* populations (Collin 2003). It is estimated that only 1 % of the elms still remain alive in Germany (Mackenthun 2004), whereas the white elm is considered an endangered species in northern Belgium (Vander Mijnsbrugge et al. 2005), southern France (Timbal & Collin 1999), and Finland (Collin et al. 2004, Vakkari et al. 2009). Moreover, many small isolated populations throughout its distribution range are at risk of genetic drift (Collin 2003). As such, this species has been identified as needing specific conservation measures in Europe (Collin et al. 2004).

According to *Flora Ibérica* (Navarro & Castroviejo 1993), *U. laevis* is an established alien species in Spain which was introduced as an ornamental; a conclusion based on its small population sizes and scarcity. This is the opinion which has prevailed among botanists, and thus, limited efforts were initially undertaken towards white elm conservation in Spain. However, the presence of *U. laevis* in Spain was cited for the first time by Lapeyrouse (1813) in the Pyrenees. Following this, it was also observed in Asturias (Pastor 1853), and as a result, was included in the first Iberian Floras (Willkomm & Lange 1861, Amo 1871). Nevertheless, other botanical studies failed to include this species (Costa 1864, Loscos & Pardo 1866, Laguna & de Ávila 1883, Ceballos 1966, Ruiz de la Torre 1971) or considered it as an introduced species (Casadevall & Font i Quer 1933). More recently, attending to several white elm stand characteristics, certain authors considered that *U. laevis* could be native to the Iberian Peninsula (Segura 1973, Aizpuru et al. 1999).

Following the second DED pandemic (Brazier 2000), several small, scattered, previously unknown populations of *U. laevis* were detected during the field surveys carried out by the Spanish Elm Conservation and Breeding Programme (SECBP, Technical University of Madrid, Spanish Environmental Ministry - Fig. 1). The location and characteristics of some of these newly located populations indicated that human introduction was highly unlikely. The fact that 41 of these 52 stands had not been previously detected was quite surprising, but can be explained by: (i) some stands growing in difficult access areas; (ii) difficulty in distinguishing *U. laevis* from field elm (*U. minor*) or wych elm (*U. glabra*) morphologically, unless the tree has flowers or fruits; and (iii) lack of interest

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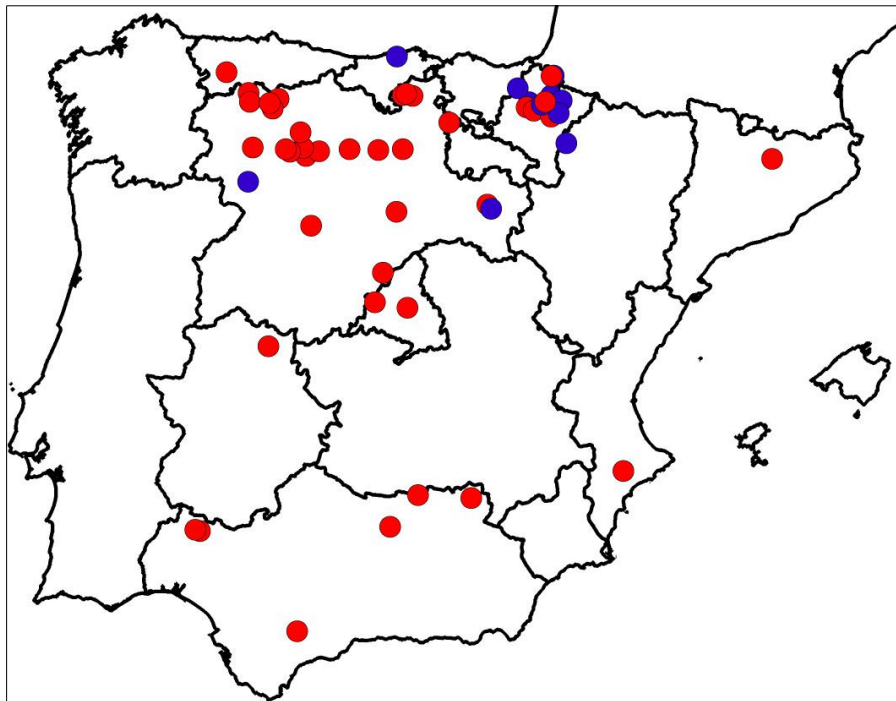


Fig. 1 - Distribution of *Ulmus laevis* populations in Spain. Populations previously cited in the literature (blue dots) are differentiated from those detected by the Spanish Elm Conservation and Breeding Programme (red dots). Modified from Venturas et al. (2013a).

in reporting its presence, given that it was considered an alien species. In addition, *U. laevis* trees were more easily detected after DED pandemics because they remained alive, whereas other elms died. Despite white elms being highly susceptible to DED (Pinon et al. 2005, Solla et al. 2005) they can survive the disease by an escape mechanism: bark beetles (*Scolytus* spp.), the propagation vectors of DED, prefer feeding on *U. minor* and *U. pumila* L. (Webber & Kirby 1983, Webber 2004) due to the chemical composition of their bark (Pajares et al. 2004, Martín-Benito et al. 2005).

Determining whether or not small marginal populations of a species are native is complicated, especially in Mediterranean riparian forests, as they have been deeply transformed by humans over the last 4000 years (Hooke 2006, Valbuena-Carabaña et al. 2010). Indeed, all elm species were initially considered to be introduced in the Iberian Peninsula due to the lack of evidence for their presence in the first fossil records (Huntley & Birks 1983). Following this, and based on taxonomic traits, Richens & Jeffers (1986) established that *U. glabra* was native to northern Spain, and considered that if *U. minor* was to be indigenous, it would only be so in the eastern half of the Iberian Peninsula. When the number of palaeobotanic records increased and *Ulmus* spp. pollen was found all over Spain (Gil & García-Nieto 1990, López 2003), fossil remains were assumed to belong to *U. glabra* in the moun-

tain areas, and to *U. minor* in the lowlands. Contrary to the hypothesis put forth by Richens & Jeffers (1986), palaeobotanic remains which appeared in non-mountainous areas of western Spain were assumed to be from *U. minor*, despite the fact that pollen and wood from European elms cannot be morphologically distinguished at species level (Schweingruber 1990, Stafford 1995). Therefore, after the discovery of new *U. laevis* populations, the following question arose: could part of the pollen from western Spain belong to *U. laevis*?

Herein, we review the process followed by SECBP to demonstrate the nativeness of *U. laevis* in Spain, and the species' natural distribution, ecology, conservation status and recovery possibilities.

Nativeness of *U. laevis* in the Iberian Peninsula

Neutral genetic markers have proved to be useful when it comes to determining the status of populations of uncertain origin. Iberian native tree populations are usually genetically differentiated from central and eastern European populations, due to isolation and limited gene flow between Pleistocene discrete glacial refugia (e.g., King & Ferris 1998, Petit et al. 2002, Heuertz et al. 2004, Magri et al. 2006). In contrast, introduced populations normally show lower genetic diversity than the populations from which they originate, and lack private alleles (Stone & Sunnucks 1993).

Ulmus laevis genetic diversity is relatively low compared to those of other tree species (Machon et al. 1995, 1997, Whiteley 2004, Vakkari et al. 2009, Nielsen & Kjær 2010). Only three chloroplast haplotypes have been identified across Europe (Whiteley 2004): haplotype *A*, the high frequency one which extends all over Europe, and two rare ones, haplotype *B*, restricted to southern France, and haplotype *C*, located in the Balkans and southwest Russia. Whiteley (2004) argued that this haplotype distribution was congruent with white elm expansion from a core glacial refugium in Russia, as proposed by Huntley & Birks (1983), but that this could also indicate the existence of additional refugia in southern European peninsulas.

Building on previously existing information (Whiteley et al. 2003a, Whiteley 2004), 20 populations from central Europe, southern France and Spain were sampled in order to determine whether Iberian populations of *U. laevis* were native (Fuentes-Utrilla 2008, Fuentes-Utrilla et al. 2014). Chloroplast (cpDNA) restriction fragment length polymorphism (RFLP) and nuclear (nDNA) microsatellite markers were analyzed. Genetic diversity indexes were calculated, and Bayesian clustering and demographic analyses were performed.

The native status of *U. laevis* in the Iberian Peninsula was supported by: (i) diversity levels, which were low but similar to other European populations; (ii) the presence of haplotypes *A* and *B*, and of nDNA private alleles in Spain; (iii) genetic differentiation and spatial genetic structure of Spanish populations; and (iv) demographic analyses which showed signs of an ancestral bottleneck (Fuentes-Utrilla 2008, Fuentes-Utrilla et al. 2014). Moreover, there is no historic information supporting *U. laevis* introduction, nor its extensive use in Spain, contrary to what happens with *U. minor* (Gil et al. 2004) or *U. pumila* (Cogolludo-Agustín et al. 2000). Therefore, the Iberian Peninsula is considered to have contained some glacial refugia for *U. laevis* (Fuentes-Utrilla 2008, Fuentes-Utrilla et al. 2014), as also shown for other European tree taxa (Petit et al. 2002, Magri et al. 2006). This interpretation is also consistent with the climatic modeling of the species' distribution, which identifies parts of the Iberian Peninsula suitable for *U. laevis* under both the Last Glacial Maximum and present day climates (Svenning et al. 2008).

Edaphic factors and *U. laevis* distribution

Calcicole species can grow normally on both calcareous and siliceous soils (Zohlen 2002). However, calcifuge species growing on calcareous soils suffer nutrient deficiencies due to a limited absorption of phosphorous (Tyler 1992, Zohlen & Tyler 2004),

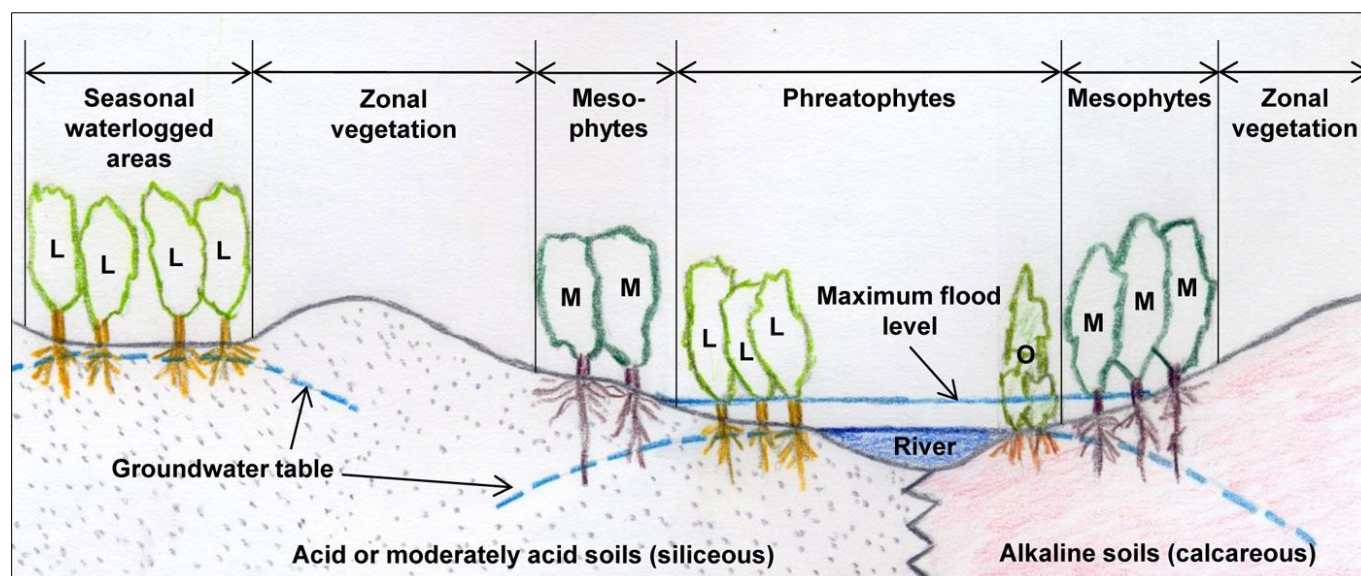


Fig. 2 - *Ulmus laevis* and *U. minor* distribution sketch in relation to soil nature and water availability. *Ulmus laevis* trees (L); *Ulmus minor* trees (M); other phreatophytes (O).

manganese (Messenger 1986, Thomas et al. 1998) and chiefly iron (Zohlen & Tyler 1997, 2000, Zohlen 2002). Iron is of great importance for many metabolic and enzymatic processes (Kobayashi & Nishizawa 2012). Iron deficiency compromises plant growth and establishment because it causes reductions in photosynthetic rates (Larbi et al. 2006). Plants have developed specialized mechanisms for increasing root iron availability and facilitating its uptake and transport within the plant (Marschner & Römheld 1994). Elms are classified as *Strategy I* plants (Marschner & Römheld 1994), and as such, their root iron uptake mechanisms are based on: (i) the production of root ferric reductase for transforming Fe^{3+} into Fe^{2+} compounds; (ii) the induction of Fe^{2+} membrane transporters; (iii) increasing iron solubility by acidifying the rhizosphere excreting protons (H^+); and (iv) increasing iron availability by secreting organic compounds (Abadía et al. 2011).

Ulmus laevis populations in Spain grow on siliceous moderately acid and acid soils, thus suggesting that this species has a calcifuge character within the region (Fig. 2). *Ulmus minor* can grow both on acid and alkaline soils, but is thought to be native to calcareous soils (Richens & Jeffers 1986). In light of this, we tested whether differences in the efficiency of root iron uptake mechanisms may account for the differential distribution of these two species in Spain (Venturas 2013, Venturas et al. 2014a).

Seedlings from both species were grown in hydroponic culture under iron uptake limiting conditions. Their growth, degree of lime-induced chlorosis symptoms, root proton extrusion capability, and root ferric reductase activity were evaluated. Results showed

that both species suffered severe lime-induced chlorosis if grown with no iron. However, re-supply of iron in *U. minor* led to a better mobilization of iron over the complete plant and leaf surface, whereas this was confined to young leaves and along the leaf nerves in *U. laevis*. Moreover, *U. laevis* seedlings showed a lower root proton extrusion capacity and root ferric reductase activity than *U. minor*. Therefore, differences in the iron acquisition mechanisms may be at least partly responsible for these species' distribution in the Iberian Peninsula, enabling *U. minor* to grow on calcareous soils where iron absorption is more limiting for *U. laevis* (Venturas 2013, Venturas et al. 2014a).

Water availability and *U. laevis*

Ulmus laevis is a riparian tree which thrives in damp soils (Collin et al. 2000, Fig. 2). An association study between species composition and soil types conducted in Estonia showed that this species grows mainly in embankments where the predominant soils are Eutric Gleysols or Gleyic Fluvisols (Paal et al. 2007). It has also been observed that *U. laevis* has better survival and growth rates than *U. minor* in heavy clay soils with prolonged waterlogging (Cicek et al. 2007). This indicates the high water demand and waterlogging tolerance of this elm species.

Wetland and flood-tolerant plants survive waterlogging due to complex anatomical, physiological, morphological, and life-history adaptations (Blom & Voesenek 1996, Kozłowski 1997, Pezeshki 2001). Xylem cavitation, for example, might help stem and root oxygen supply in flooded *U. laevis* plants (Venturas et al. 2013b). In a recent study, seedlings of *U. laevis* subjected to experimental waterlogging exhibited 40% loss

of root hydraulic conductivity relative to control, well-watered plants. Most likely in relation to this, stomata partly closed and net photosynthesis was reduced. Respiration rates of leaves, stems and roots increased soon after waterlogging started, so that net carbon gain at the plant level was severely diminished. However, seedlings survived two months of waterlogging and recovered normal water-transport capacity and net photosynthesis afterward. This indicated that *U. laevis* is sensitive but considerably resistant to waterlogging at the seedling stage (Li et al., unpublished data).

Drought-induced hydraulic failure affects plant productivity and survival (Sperry et al. 2008, López et al. 2013, Barigah et al. 2013), and the European white elm has been shown to be highly susceptible to drought-induced xylem cavitation (Venturas et al. 2013b). Large xylem vessels confer this species' high water transport capacity but counter its resistance to drought, thus supporting the trade-off between waterlogging and drought tolerance observed across species (Niinemets & Valladares 2006). Therefore, the expected aridification of the Iberian Peninsula (Somot et al. 2008) could further compromise the survival of *U. laevis* populations (Allen et al. 2010, Hemery et al. 2010), as this will probably increase water demand for irrigation, causing further depletion of water tables, and increased drought episodes. A drought-stress experiment carried out with plants from France, Sweden and Germany showed that there is substantial additive genetic variation for drought adaptation in *U. laevis* populations (Black-Samuelsson et al. 2003). This has also been observed for other adaptive traits such as growth and leaf phenology (Whiteley et al. 2003b). Therefore,

there is a genetic basis for *U. laevis* adaptation to future water availability changes (Black-Samuelsson et al. 2003, Hemery et al. 2010), and Mediterranean populations may well be an important resource for breeding programmes.

Reproductive ecology

Ulmus laevis is an anemophilous, self-incompatible (Mitttempergher & La Porta 1991), and highly outcrossing species (Nielsen & Kjær 2010). Its fruits are samaras (winged nuts) with ciliated margins, which are dispersed by both wind (anemochory) and water (hydrochory - Collin 2003). Dispersal by two or more agents (diplochory) increases dispersal benefits and decreases seed mortality probabilities (Vander Wall & Longland 2004). Wind disperses 95 % of *U. laevis* seeds at short distances (less than 30 m), thus enabling them to reach suitable microhabitats close to mother trees, or landing on a water surface for secondary transport. In contrast, hydrochory allows long-distance gene exchange and the colonization of new sites (Venturas et al. 2014b). In some *U. laevis* stands, a marked spatial genetic structure can be found due to the low wind dispersal distance (Nielsen & Kjær 2010, Venturas et al. 2013a) and the lack of secondary seed movement (Venturas et al. 2014b).

In riparian species, seed release timing is very important for seed dispersal and seedling establishment (Deiller et al. 2003, Nilsson et al. 2010). In the Iberian Peninsula samara abscission occurs from mid-April to the end of June. Therefore, samara dispersal usually occurs just after spring floods, when the conditions are optimal for seed germination and seedling establishment as the pre-existing vegetation is eliminated with the floods, and mud is deposited as water returns to the main channels (López-Almansa 2004, Nilsson et al. 2010). Samara release rates mainly depend on maturity (phenology) and increase with strong winds, but not with rain (Venturas et al. 2014b). White elm seeds germinate soon after they are dispersed and show high germination rates (Çiçek & Tilki 2005, SECBP, unpublished data).

Ulmus laevis is a masting species. A three year study performed in a population from central Spain showed that, in a mast year, seed production could be 24 times higher than during a non-mast year. As a result, the mast year maximum seed rain was 9020 seeds m⁻², whereas in the lowest seed production year, this value only reached 8 seeds m⁻² (Venturas et al. 2014b). Increased pollination efficiency in anemophilous species, and satiation of seed predators, are two factors which often favor the development of masting (Kelly & Sork 2002). Taking into consideration that the spatial distribution of *U. laevis* has never been large, it is unlikely that this species could control seed predator

populations by masting, especially not those of highly mobile seed predators such as birds, which are attracted by large seed crops (Perea et al. 2013). In light of this, masting probably evolved as a result of increased pollination efficiency in *U. laevis* (Venturas et al. 2014b).

Seed predation is an important selective pressure which drives the evolution of seed characteristics (Janzen 1969). Parthenocarpy and empty fruit formation, which are common in elms (López-Almansa & Gil 2003, López-Almansa et al. 2004), act as a mechanism that enhances plant fitness by reducing pre- and post-dispersal seed predation (Ghazoul & Satake 2009, Perea et al. 2013). Birds are the main pre-dispersal predators, consuming up to 98 % of full seeds in non-mast years (Venturas et al. 2014b). Rodents are the main post-dispersal predators, and can cause local seed extinction, especially under shrub cover, which is their favorite microhabitat (Hulme & Borelli 1999, Hulme & Hunt 1999, Perea et al. 2013). Therefore, open microhabitats created by floods are also of great importance to recruitment from a seed survival perspective (Venturas et al. 2014b).

Vegetative propagation mechanisms (root suckers and stool-shoots) may be important for *U. laevis* regeneration and colonization of new sites after flooding disturbance in riparian formations (Collin 2003, Deiller et al. 2003). No root-suckers were observed in two Spanish wetland stands, but stool-shoots could have helped these populations to maintain genetic diversity levels after tree felling (Venturas et al. 2013a).

Conservation of Spanish populations

Spanish *U. laevis* populations are vulnerable to genetic drift, bottlenecks and stochastic events due to their small size and fragmentation (Fuentes-Utrilla et al. 2014). However, the greatest risk for these populations is human-induced habitat transformation. For example, the population of Palazuelos de Eresma (Segovia - PAL in Fig. 3) lost 22 % of its mature elms and cannot naturally regenerate because it was transformed into a golf course and housing complex (Venturas et al. 2013a, Fuentes-Utrilla et al. 2014). Valdelatas stand (Madrid - VAL in Fig. 3) lacks sufficient recruitment due to underground water-table loss caused by overexploitation of Madrid's aquifer (Venturas et al. 2013a, 2014b). Flow regulation of Mediterranean rivers also negatively affects the dispersal, recruitment and establishment of hardwoods due to decreased water discharge and increased flood control after damming (Nilsson & Bergren 2000, Nilsson et al. 2010, Bejarano et al. 2012). Long term conservation of *U. laevis* requires restoration of hydrological regimes, and the re-establishment

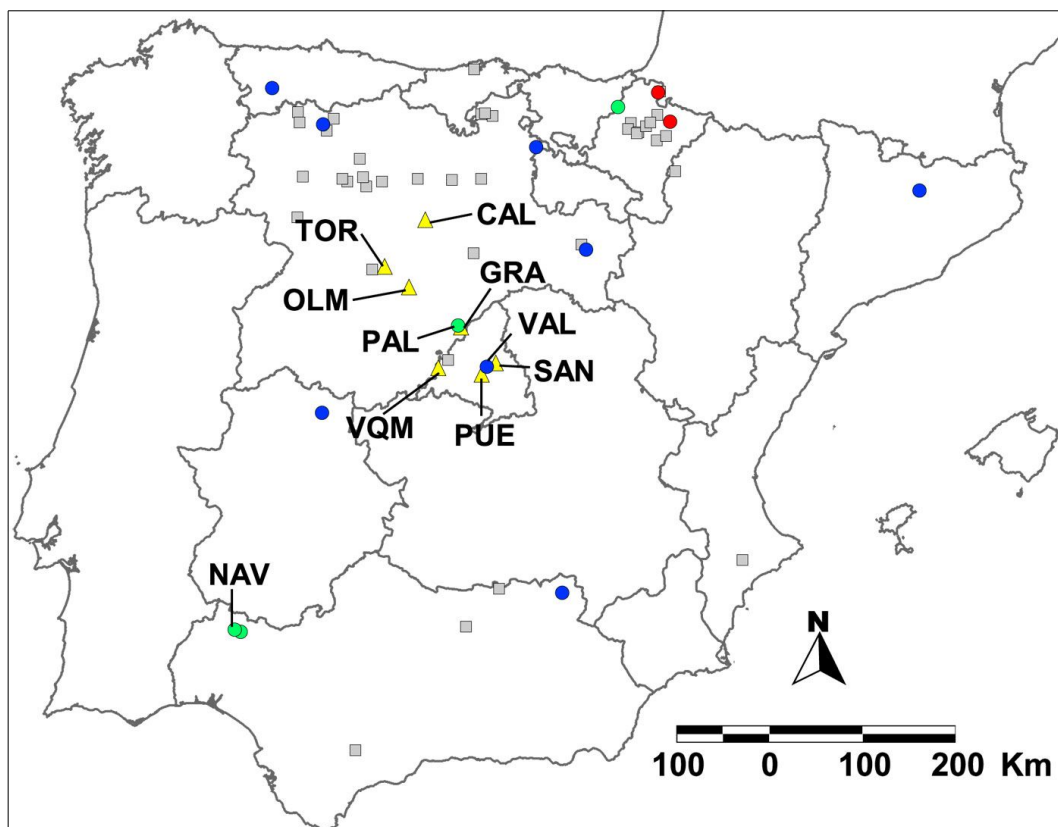
of ecological patterns and processes where they have been destroyed by humans (Howe & Miriti 2004), taking into consideration landscape ecology concepts (Laforteza et al. 2013).

According to the International Union for Conservation of Nature's (IUCN) Red List Criteria (IUCN 2001) *U. laevis* should be considered as "critically endangered" in the Iberian Peninsula because: (i) it is native; (ii) its populations cover an area smaller than 10 km²; and (iii) it is suffering a decline in habitat quality and number of adult individuals (Fuentes-Utrilla et al. 2014). In light of this, SECBP is currently working for the inclusion of *U. laevis* in the Red List of Spanish Vascular Flora (Anonymous 2000), thus meaning it would be protected by national laws. Moreover, Mediterranean riparian forests with *U. laevis* should be included as a "natural habitat type of community interest", under Section 92 of the Habitat and Species Directive (Council Directive 92/43/EEC), in order to strengthen *U. laevis* conservation within Natura 2000 Network (Fuentes-Utrilla et al. 2014).

The first steps towards conservation of Spanish *U. laevis* populations have already been initiated by the SECBP. An inventory of the occurrence of the species is the first prerequisite for establishing any gene conservation programme (Eriksson 2001). SECBP already has an inventory of the populations, but it is still gathering more information on *U. laevis* occurrence, abundance and stand characteristics. Acquiring genetic information is of great importance when it comes to ensuring genetic variation is withheld in conservation programmes (Eriksson 2001, Goodall-Copestake et al. 2005). It is also necessary for defining evolutionary significant units, and management units within these, upon which conservation measures should be based (Moritz 2002). Genetic knowledge regarding certain Spanish white elm populations has served well to define management units (Fuentes-Utrilla et al. 2014). However, it would be interesting to complete the analyses with populations which have not yet been sampled (Fig. 3). For example, a recent survey on the population of Las Navas (Huelva - NAV in Fig. 3) has shown that it is constituted by trees with both haplotypes A and B, extending further south the presence of haplotype B (Diego Maya & SECBP, unpublished data).

Several *in situ* and *ex situ* conservation measures have been proposed for elms (Collin et al. 2004). Whenever possible, *in situ* conservation should be carried out as it enables dynamic adaptation. To avoid the potential loss of additive variance, the effective population size (N_e) to preserve should be larger than 50. Conversely, *in situ* stands should contain 150-200 individuals (Eriksson 2001). *In situ* conservation is currently

Fig. 3 - Spanish *Ulmus laevis* populations' genetic knowledge and *ex situ* conservation sites. Populations on which genetic studies have been performed (circles), populations on which genetic knowledge is lacking (grey squares) and *ex situ* conservation sites (yellow triangles). Populations with chloroplast DNA (cpDNA) haplotype A (blue circles); populations with cpDNA haplotype B (red circles); populations containing both A and B cpDNA haplotypes (green circles). Data: Fuentes-Utrilla et al. (2014), Venturas et al. (2013a), and SECBP unpublished data.



only being carried out in Valdelatas (Madrid). As N_e has been estimated at approximately 30 individuals (Venturas et al. 2013a), the first measure taken was to increase population size (53 mature trees) using seedlings grown from seeds collected in the stand. *Ex situ* conservation of Valdelatas is also being implemented by planting seedlings from this provenance in the Viñuelas stream (350 individuals; San Sebastián de los Reyes, Madrid - SAN in Fig. 3), and in the gardens (90 individuals) of Valdequemada municipality (Madrid - VQM in Fig. 3). SECBP has already established three seed-orchards with approximately 300 seedlings, each belonging to 65 families from Palazuelos de Eresma (Segovia - PAL in Fig. 3). These are located in Calabazanos (Palencia - CAL in Fig. 3), Tordesillas (Valladolid - TOR in Fig. 3) and La Granja de San Ildefonso (Segovia - GRA in Fig. 3). A re-forestation scheme with 2220 individuals from 18 families of Palazuelos de Eresma has also been carried out at the confluence of Adaja and Eresma rivers (Olmedo, Valladolid - OLM in Fig. 3), in order to allow for dynamic *ex situ* conservation. A few genotypes (37) from nine Spanish provenances have also been planted in the conservation orchard of Puerta de Hierro (Madrid - PUE in Fig. 3). Furthermore, *in situ* conservation activities should also be carried out to increase the size of other populations. Optimizing canopy irradiation by thinning has been propo-

sed as an appropriate method to increase elm stand vitality in the Czech Republic (Srámek & Cermák 2012). Despite Iberian white elm stands having a different structure, the felling of competing vegetation might help increase elms' vitality, and create clearings in the riparian forest where elm seedlings can establish themselves.

Cryopreservation of seeds is a relatively cheap and easy static way in which to preserve the genetic resources of *U. laevis* (Collin et al. 2004). Whilst there is a European cryobank with *Ulmus* spp. resources (Harvenget et al. 2004), it does not contain *U. laevis* from Spain because at the time when the bank was established the *taxon* was not yet considered an indigenous species. Future work should focus on cryopreserving seeds from a wide range of Spanish *U. laevis* populations.

Finally, the conservation of *U. laevis* would produce extra benefits beyond the species' conservation itself, particularly when it occurs in a multifunctional landscape. *Ulmus laevis* has been identified as a good choice for floodplain reforestations (Mackenthun 2004) because it is less likely to be affected by DED than *U. minor* (Weber 2004), and due to its ability to survive long flooding periods (Collin 2003). The latter is an important issue for forest planning as extreme flooding events are expected to occur more frequently in central and western Europe as a consequence of climate change (Glenz et al. 2006, Kramer et al. 2008).

Restoration of river banks with *U. laevis* could also be beneficial for the conservation of granivorous fauna due to the large seed-crops it produces even in non-mast years (Perea et al. 2013, Venturas et al. 2014b). White elm has been shown to be important for the conservation of epiphytic bryophyte and lichen communities in Latvia (Mežaka et al. 2012), as well as for millipede (Diplopoda) communities in Slovakia (Stašiov et al. 2012). Moreover, extracts from *U. laevis* may also be useful for developing drugs against cancer (Paschke et al. 2009, Hartmann et al. 2011). Conservation activities are now more likely to occur and succeed since all of the research work outlined above has led to confirmation of *U. laevis*' autochthonous status and made it possible to delineate its ecology in the Iberian Peninsula.

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In memoriam of Margarita Burón. She was the first member of SECBP to consider that *U. laevis* could be native to Spain.

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